

# Stoichiometric patterns in foliar nutrient resorption across multiple scales

Sasha C. Reed<sup>1</sup>, Alan R. Townsend<sup>2</sup>, Eric A. Davidson<sup>3</sup> and Cory C. Cleveland<sup>4</sup>

<sup>1</sup>US Geological Survey, Southwest Biological Science Center, Moab, UT 84532, USA; <sup>2</sup>INSTAAR & Department of Ecology and Evolutionary Biology University of Colorado, Boulder, CO 80309, USA; <sup>3</sup>The Woods Hole Research Center, Falmouth, MA 02540, USA; <sup>4</sup>Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA

## Summary

Author for correspondence:

Sasha C. Reed

Tel: +1 435 210 4824

Email: screed@usgs.gov

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- Nutrient resorption is a fundamental process through which plants withdraw nutrients from leaves before abscission. Nutrient resorption patterns have the potential to reflect gradients in plant nutrient limitation and to affect a suite of terrestrial ecosystem functions.
- Here, we used a stoichiometric approach to assess patterns in foliar resorption at a variety of scales, specifically exploring how N : P resorption ratios relate to presumed variation in N and/or P limitation and possible relationships between N : P resorption ratios and soil nutrient availability.
- N : P resorption ratios varied significantly at the global scale, increasing with latitude and decreasing with mean annual temperature and precipitation. In general, tropical sites (absolute latitudes < 23°26') had N : P resorption ratios of < 1, and plants growing on highly weathered tropical soils maintained the lowest N : P resorption ratios. Resorption ratios also varied with forest age along an Amazonian forest regeneration chronosequence and among species in a diverse Costa Rican rain forest.
- These results suggest that variations in N : P resorption stoichiometry offer insight into nutrient cycling and limitation at a variety of spatial scales, complementing other metrics of plant nutrient biogeochemistry. The extent to which the stoichiometric flexibility of resorption will help regulate terrestrial responses to global change merits further investigation.

## Introduction

Understanding and predicting the nature and extent of nutrient limitation to net primary production (NPP) is a central topic in modern ecology. For example, a robust understanding of nutrient controls over NPP is increasingly important in the forecasting of terrestrial ecosystem responses to multiple global changes, as is an understanding of which nutrient(s) are limiting and how limitation varies across spatial and temporal scales (Hungate *et al.*, 2004; Thornton *et al.*, 2009; Vitousek *et al.*, 2010; Reed *et al.*, 2011b; Townsend *et al.*, 2011). Several recent data syntheses from nutrient manipulation experiments have indicated that NPP is commonly limited by nitrogen (N) and/or phosphorus (P) availability (Elser *et al.*, 2007; LeBauer & Treseder, 2008; Harpole *et al.*, 2011). However, direct tests of nutrient limitation in the field are notably difficult, especially in high-diversity forests, and all methods have strengths and limitations (Cleveland *et al.*, 2011). Long-term field fertilization experiments are often considered the best approach for assessing nutrient limitation, yet significant logistical challenges and extended response times (among other things) have precluded their repeated use in many terrestrial biomes (Elser *et al.*, 2007; Harpole *et al.*, 2011).

The difficulty of measuring nutrient limitation to plant growth in the field creates the need for more tractable proxies of potential limitation status. Some previous efforts to identify such metrics have focused on foliar nutrient stoichiometry, and data suggest that foliar N : P ratios do, on some scales and in some ecosystems, vary with soil N and P availability and offer predictive insight into nutrient limitation to plant productivity (e.g. Koerselman & Meuleman, 1996; Güsewell & Koerselman, 2003; Tessier & Raynal, 2003; Güsewell, 2004; Richardson *et al.*, 2004; Reich & Oleksyn, 2004). However, other data suggest that foliar N : P ratios do not consistently predict nutrient limitation (e.g. Ostertag, 2010), and that local-scale species or temporal variation may mask or even overwhelm broader scale patterns (Townsend *et al.*, 2007).

Litterfall mass and nutrient analyses may also provide insight into nutrient limitation. For example, Vitousek (1982, 1984) used data from a range of forests to show that low-nutrient sites produced higher litterfall dry mass : nutrient ratios relative to nutrient-rich sites, thus maintaining a higher nutrient use efficiency. Litter dry mass : nutrient ratios (Vitousek, 1982, 1984) and litter N : P ratios (McGroddy *et al.*, 2004) suggest that N is cycled more efficiently in temperate and montane tropical forests, and P more efficiently in many lowland tropical forests, which is

consistent with the presumed geographic variations in N vs P limitation (i.e. N limitation in temperate and high-latitude systems and P limitation in the lowland tropics). However, although patterns in litterfall stoichiometry may reflect nutrient use and cycling, they do not directly assess nutrient resorption patterns. Thus, across a range of scales, many important questions remain. How does nutrient resorption drive the observed patterns in litterfall nutrient concentrations? Does the stoichiometry of nutrient resorption offer insight into nutrient limitation? How could variability in nutrient resorption help to regulate terrestrial responses to global environmental change?

Previous work has suggested that patterns in foliar nutrient resorption (also called nutrient retranslocation or reabsorption) may offer insight into plant nutrient status and limitation (e.g. Nye, 1961; Stachurski & Zimka, 1975; Turner, 1977; Pugnaire & Chapin, 1993; Bowman, 1994; Enoki & Kawaguchi, 1999; Van Heerwaarden *et al.*, 2003b; Güsewell, 2004; Kitayama *et al.*, 2004; Richardson *et al.*, 2008), although the utility of this metric has also been called into question (e.g. Chapin, 1980; Lajtha & Klein, 1988; Chapin & Shaver, 1989; Aerts, 1996; Vitousek, 1998). Most studies have focused on whether plants in nutrient-poor environments resorb more nutrients than plants in nutrient-rich environments, a pattern that would make sense from a nutrient economics perspective (Grime, 1979; Chapin, 1980; Berendse & Aerts, 1987; Aerts, 1990; May & Killingbeck, 1992). Nutrients resorbed during senescence are directly available for subsequent plant use, reducing a plant's dependence on external nutrient uptake from the environment (Clark, 1977; Turner, 1977). In this way, resorption is a central component of any plant's nutrient acquisition strategy (with plants commonly resorbing > 50% of foliar N and P; Aerts, 1996; Vergutz *et al.*, 2012), and contributes directly to plant nutrient use efficiency (Vitousek, 1982; Aerts & Chapin, 2000; Franklin & Ågren, 2002).

Because litterfall represents the largest source of nutrients to the forest floor (Moore & Braswell, 1994; Currie, 2003), the 'resorption valve' helps to determine the stoichiometry of litter inputs, and thus plays a significant role in regulating a range of other belowground ecosystem processes. For example, a plant with relatively high nutrient resorption efficiency could produce relatively low-quality litter, which, in turn, could reduce litter decomposition and nutrient mineralization rates (Gosz *et al.*, 1976; Melillo *et al.*, 1982; Vitousek, 1982; Aerts, 1997), and affect fundamental ecosystem processes, including soil respiration, denitrification and N fixation, among others (Davidson *et al.*, 1993; Vitousek & Hobbie, 2000; Cleveland & Townsend, 2006; Reed *et al.*, 2011a). As such, a quantitative understanding of nutrient resorption patterns and mechanisms may be essential for the effective modeling of nutrient cycling and NPP at a range of scales (Jackson *et al.*, 1997; Vergutz *et al.*, 2012), and for the evaluation of how flexibility in resorption (or a lack thereof) helps to determine terrestrial ecosystem responses to global change (e.g. Norby *et al.*, 2000; Norby & Iversen, 2006; Aerts *et al.*, 2007).

Accurate assessments of nutrient resorption are a critical component of the measurement's utility, and issues such as the reduction in leaf mass and size during senescence are a concern

(Van Heerwaarden *et al.*, 2003a; Vergutz *et al.*, 2012). For example, Vergutz *et al.* (2012) used a global meta-analysis to create a mass loss correction factor (MLCF) accounting for the error introduced into resorption estimates by changing mass between green and senesced leaves. Their analysis showed resorption values for N and P that were higher than previous estimates (62.1% and 64.9% for N and P, respectively, compared with 50% and 52% from uncorrected data; Aerts, 1996). However, a stoichiometric perspective on nutrient resorption may overcome some of the issues associated with leaf measurement. For example, in the analysis by Vergutz *et al.* (2012), although the correction significantly altered the amount of N or P being resorbed, it did not change the relationship between N and P resorption at the global scale, suggesting that a stoichiometric approach could help to reduce the error associated with mass loss.

Here, we set out to explore patterns in nutrient resorption stoichiometry – in particular for N and P – across multiple scales. We drew from existing syntheses that have focused on patterns of single-element nutrient resorption (e.g. Yuan & Chen, 2009) to assess the broad geographical patterns and variation in N : P resorption ratios. We then further refined the analysis and focused on stoichiometric resorption patterns in the tropical forest biome for three key reasons. First, although several recent analyses have reported global variations in plant nutrient status, these analyses have included relatively few data from tropical ecosystems (Aerts, 1996; Reich & Oleksyn, 2004; Elser *et al.*, 2007). Next, tropical forests play a critical role in a range of global-scale processes, including carbon (C) and N cycling, and an understanding of nutrient cycling and limitation there has significant global change implications (Hedin *et al.*, 2009; Cleveland *et al.*, 2011; Reich, 2011; Townsend *et al.*, 2011; Davidson *et al.*, 2012; Wood *et al.*, 2012). Finally, research suggests that the nature of nutrient limitation in the tropics may be fundamentally different from that in the temperate zone, yet few direct tests of nutrient limitation exist, restricting our ability to predict how and where nutrient limitation may constrain tropical ecosystem responses to global change. Our two primary goals were to assess patterns in the N : P ratio of resorption efficiency at multiple scales, and to explore the causes and consequences of such patterns within the context of nutrient limitation.

## Materials and Methods

We addressed our objectives in three ways. First, we conducted a meta-analysis assessing patterns in N : P resorption efficiency ratios using assembled data from the literature (e.g. Aerts, 1996; Kobe *et al.*, 2005; Yuan & Chen, 2009) and by searching the references therein. We conducted searches using online databases and search engines (including ISI Web of Knowledge and Google Scholar) with the search terms nitrogen, nutrient, phosphorus, reabsorption, resorption, retranslocation and translocation. All data were obtained from the publicly available, peer-reviewed literature. For the global synthesis, we excluded data from plants < 20 yr old (as storage and internal nutrient cycling can change significantly at earlier stages of plant growth; Miller, 1995). We also excluded managed sites and glasshouse experiments,

epiphytes, and data from mangroves and wetlands. In addition, unlike some of the reviews we utilized, we included data from the literature for graminoids, N<sub>2</sub>-fixing plants and resorption efficiencies that ignored species identity (e.g. Kitayama *et al.*, 2004). For studies that reported resorption efficiencies from one site for more than one time point, we took an average; for example, if resorption was assessed in three consecutive years, we averaged the three efficiencies to create a single resorption value. To ensure data comparability, we only used data from papers in which the authors specifically indicated that leaf litter samples were collected either from litter traps or from newly shed leaves that fell naturally or by shaking plants. Resorption efficiency was always calculated as described by Killingbeck (1996).

$$\frac{X_{\text{Gr}} - X_{\text{Sen}}}{X_{\text{Gr}}} \times 100$$

( $X_{\text{Gr}}$ , N or P concentration of green foliage;  $X_{\text{Sen}}$ , N or P concentration of senesced leaves). For statistical analyses and graphing, we also used the natural logarithm of the N : P resorption efficiencies:

$$\log_e \left( \frac{(N_{\text{Gr}} - N_{\text{Sen}})/N_{\text{Gr}}}{(P_{\text{Gr}} - P_{\text{Sen}})/P_{\text{Gr}}} \right)$$

( $N_{\text{Gr}}$  and  $P_{\text{Gr}}$ , green foliage N and P concentrations, respectively;  $N_{\text{Sen}}$  and  $P_{\text{Sen}}$ , senesced leaves, N and P concentrations, respectively).

Second, we explored data from a forest age chronosequence in the Sao Francisco do Para region of Brazil where, except for the mature forest (which was conservatively estimated at 200 yr old), all forests were regrowing after abandonment of crop fields (Davidson *et al.*, 2007). Although the original manuscript described three sets of chronosequences, here we focused solely on the Sao Francisco do Para chronosequence because it alone contained the foliar P data we needed to calculate P resorption efficiencies: data were available for forests of 6, 20, 40 yr and mature ages. Although we excluded plants < 20 yr old in our global database, we did assess the 6-yr-old forest in this instance, keeping in mind the limitations of data from this time point. N and P resorption efficiencies were calculated using the equations above. More detailed site descriptions and sample processing methods can be found in Davidson *et al.* (2007).

Finally, we examined small-scale (i.e. species-level) variations in resorption by collecting a set of foliar and litter samples from a mature, lowland tropical wet forest site (*sensu* Holdridge *et al.*, 1971) located in the Golfo Dulce Forest Reserve on the Osa Peninsula in southwest Costa Rica (8°43'N, 83°37'W). The site is a stratified, closed-canopy, highly diverse forest (100–200 tree spp./ha; Kappelle *et al.*, 2002) that includes many common neotropical tree species. Soils at the site are Ultisols (Berrange & Thorpe, 1988; Bern *et al.*, 2005) and P limitation to ecosystem processes has been documented (Cleveland & Townsend, 2006; Reed *et al.*, 2007; Wieder *et al.*, 2009). As described in Reed *et al.* (2008), sunlit canopy leaves, recently abscised leaves in litter traps, bulk leaf litter from the forest floor and topsoil were collected for eight individuals each of six different tree species

(48 individuals in total) in June 2006. Live foliage was collected using a 12-gauge shotgun and fully senesced leaves were collected from trees using 2.25-m<sup>2</sup> litter traps constructed and placed next to each of the 48 trees, 5 d before litter trap collection. Species-specific abscised leaves were separated from the bulk material collected over the 5-d period, such that only leaves from the species associated with that litter trap were collected. Soils were collected as cores to a depth of 2 cm beneath the canopy of each tree.

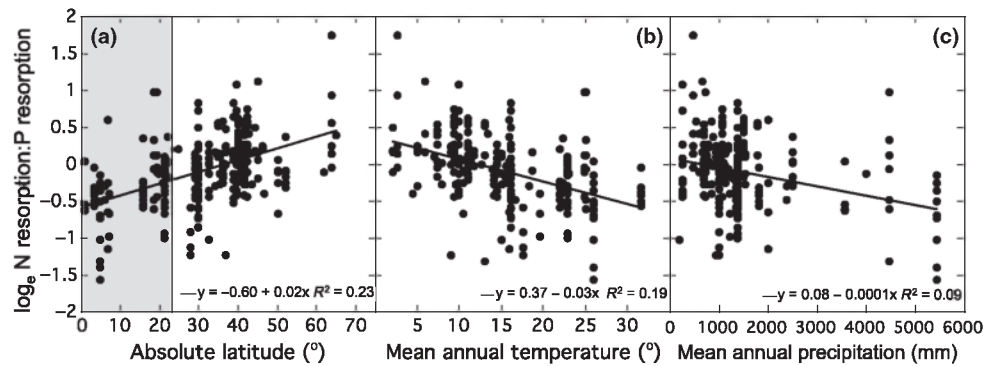
In the laboratory, foliage and litter samples were dried, ground to a fine powder, oven dried and analyzed for total C and N using a Carlo Erba EA 1110 elemental analyzer (CE Elantech, NJ, USA). Total foliar P was analyzed for oven-dried samples using a concentrated sulfuric acid/hydrogen peroxide digest and an ascorbic acid molybdate colorimetric analysis (Kuo, 1996). Soil samples were dried, sieved to 4 mm, oven dried and analyzed for total C and N on a Carlo Erba EA 1110 elemental analyzer. Extractable ammonium (NH<sub>4</sub><sup>+</sup>) and nitrate (NO<sub>3</sub><sup>-</sup>) concentrations were determined using fresh soils (also sieved to 4 mm) and a 2 M KCl extraction (Robertson *et al.*, 1999), and samples were measured colorimetrically. Soil extractable P was determined using a resin and a 0.5 M sodium bicarbonate extraction, and samples were measured colorimetrically. More detailed methods can be found in Reed *et al.* (2008). N and P resorption efficiencies were calculated using foliar and litter trap N and P concentrations and the equations above.

## Data analysis

All data were tested for normality and homoscedasticity (using Levene's test for the equality of variances); if either assumption was violated, data were log<sub>e</sub> transformed before analysis. We used simple and multiple regression analyses to examine the relationships between latitude, mean annual temperature (MAT), mean annual precipitation (MAP) and N : P resorption efficiency ratios. For the Costa Rican data, significant differences in N : P resorption ratios were assessed using ANOVA and least-significant difference (LSD) *post-hoc* analyses. Relationships between N and P resorption and N and P of other site characteristics (e.g. soil N concentrations) were assessed using bivariate correlation and nonlinear regression analyses. Significance was determined at  $\alpha < 0.05$  and all data were analyzed using SPSS 15.0 (Chicago, IL, USA).

## Results and Discussion

At the global scale, N : P resorption ratios increased with latitude and decreased with MAT and MAP (Fig. 1;  $P < 0.001$  for each). Beyond any direct effects of climate on plant physiology, such variation in the balance between N and P resorption may reflect variation in soil type and nutrient status (Reich & Oleksyn, 2004). Less weathered soils – such as those common in temperate and high-latitude regions – are thought to be more N limited, whereas more highly weathered soils – such as those common in the tropics – are thought to be more P limited. The N : P resorption patterns shown here match well with studies suggesting, in general, that weathered tropical soils tend to be



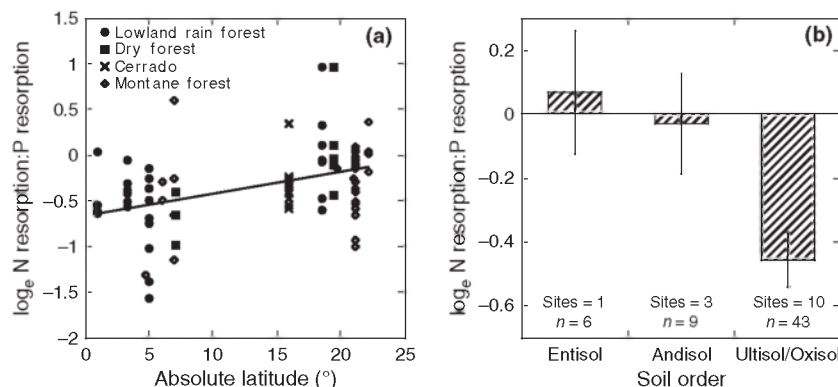
**Fig. 1** N : P resorption efficiency ratios ( $\log_e (N_{\text{resorption}}/P_{\text{resorption}})$ ) in relation to absolute latitude ( $^{\circ}$ ) (a), mean annual temperature ( $^{\circ}\text{C}$ ) (b) and mean annual precipitation (mm) (c). Tropical regions (defined as absolute latitudes  $\leq 23^{\circ}26'$ ) are shaded gray in (a). Equations depict relationships based on linear regression analyses ( $P < 0.001$  for each).

relatively N rich but P poor (Vitousek & Sanford, 1986; Vitousek & Farrington, 1997; Sollins, 1998; Martinelli *et al.*, 1999; Hedin *et al.*, 2003). They are also consistent with global patterns of foliar N : P ratios (Reich & Oleksyn, 2004), and with relationships between foliar and soil P concentrations (Ordoñez *et al.*, 2008; Cleveland *et al.*, 2011). When taken together, the data provide a range of indirect evidence suggesting that plants in comparatively N-rich and P-poor areas (e.g. many tropical rain forests) should be under selective pressure to use P more efficiently relative to N (Vitousek, 1984).

That said, not all past analyses of nutrient resorption have supported the idea that resorption efficiency is higher in low-fertility ecosystems (Chapin, 1980; Aerts, 1996). How can we resolve our results with those of previous reviews that did not see relationships between resorption and estimates of nutrient availability and status? One possibility is that, with more data now available, particularly from tropical ecosystems, larger scale patterns are easier to discern. It is also possible that viewing resorption through a 'stoichiometric lens' offers insights which the patterns of each individual nutrient cannot. For example, although our average values for N and P resorption (49% and 50%, respectively) were quite close to the averages shown in a

previous review by Aerts (1996) (50% and 52%, respectively), we observed a notable switch in N : P resorption ratios across latitudes: N : P resorption ratios were generally  $< 1$  in latitudes  $< 23^{\circ}26'$  and site averages were  $> 1$  in latitudes  $> 23^{\circ}27'$ . Nevertheless, although global-scale patterns of N : P resorption are clear (Fig. 1a), past work shows that global patterns in foliar characteristics can disappear at regional scales, highlighting the need to explore such patterns at a range of scales, especially within high-diversity ecosystems, such as the tropical forest biome (e.g. Townsend *et al.*, 2007).

As such, we focused on the tropical portions of our global dataset in order to explore how N : P resorption ratios varied along gradients within the tropics (absolute latitudes of  $< 23^{\circ}27'$ ). Despite fewer data and a restricted latitudinal range, a significant relationship between latitude and N : P resorption ratios persisted (Fig. 2a;  $P < 0.001$ ). However, in contrast with analyses of the full dataset (Fig. 1b,c), tropical N : P resorption ratios did not vary significantly with MAT ( $P = 0.965$ ) and the relationship with MAP was only marginally significant ( $P = 0.089$ ). Although soil order information was only reported for 14 of these tropical sites, including only a single site with Entisols, the data suggest that soil type may, at least in part, help to explain N : P



**Fig. 2** (a) Tropical N : P resorption efficiency ratios ( $\log_e (N_{\text{resorption}}/P_{\text{resorption}})$ ) grouped by tropical biome (lowland rain forest, dry forest, cerrado and montane forest). Linear regression results for all data together show that N : P resorption ratios increase with latitude ( $P < 0.001$ ;  $R^2 = 0.169$ ). (b) Soil order information was available for a subset of data shown in (a) and shows significantly lower N : P resorption ratios in highly weathered soils compared with Entisol and Andisol soils ( $P = 0.01$ ). Values are means  $\pm$  SE, and the number of sites and number of data points ( $n$ ) that comprise each mean are given for each soil order.

resorption efficiency ratios. In particular, data suggest that more weathered soils (e.g. Oxisols and Ultisols; 10 sites) maintained plants that resorbed much more P relative to N (Fig. 2b). Further, 82% of the tropical data at latitudes below 10° were from soils classified as ‘highly weathered’ (compared with 35% for latitudes above 10°), potentially helping to explain the latitudinal gradient seen within tropical sites (Fig. 2a). However, more data are clearly needed to help to determine how soil order and nutrient availability interact with resorption within tropical systems.

Next, we explored the variation in the stoichiometry of nutrient resorption along a successional gradient within a common region. Along a chronosequence of regenerating forests in the eastern Amazon Basin, Davidson *et al.* (2007) reported a transition from apparent N limitation in younger forests to P limitation in mature forests. Data from this chronosequence offered an opportunity to compare variations in nutrient resorption with previously established patterns in nutrient cycling along the forest age gradient. Both N and P resorption were consistently higher in the 6-yr-old forest than in either the 20- or 40-yr-old forests, although some patterns in the 6-yr-old forest could be attributed to trees being at earlier growth stages (Miller, 1995; Table 1). Across all forest ages, N resorption was highest in the youngest forest, whereas P resorption was greatest in the mature forest (Table 1). This result was driven by a diverging pattern between N and P resorption at the latest stages of succession: over the course of succession, N resorption efficiency leveled off, but P resorption continued to increase with forest age. This resulted in the lowest N : P resorption ratios in the mature forest (Table 1). Similar patterns have been observed along gradients of soil N and P availability where soil nutrients were directly assessed (e.g. Enoki & Kawaguchi, 1999; Kitayama *et al.*, 2004; Richardson *et al.*, 2008; He *et al.*, 2011), supporting the idea of links between soil nutrient status and plant recycling along local and regional gradients.

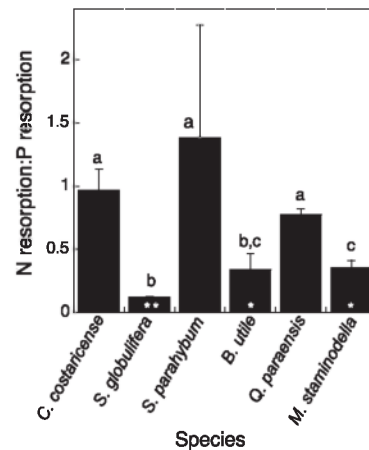
However, if, indeed, these recovering Amazon forests represent a transition from N to P limitation, an index based on a nutrient resorption stoichiometric ratio of > 1 or < 1 would not have been accurate. Across all sites, N : P resorption ratios were always < 1, demonstrating that more P was consistently resorbed relative to N in every forest age measured (Table 1). In addition, foliar N : P ratios were always above the suggested P limitation breakpoint of 16 (Koerselman & Meuleman, 1996) and were 29, 27, 34 and 32 in the 6-, 20-, 40-yr-old and mature forests, respectively. Thus, although overall patterns in foliar and resorption N : P ratios moved in the direction expected with a transition from N to P limitation, the data also suggest the need for caution in applying a given numeric threshold as an index of nutrient limitation.

Data from Costa Rica also support the idea that mature lowland tropical rain forests on highly weathered P-poor soils may generally resorb more P relative to N (Fig. 3). When all the data from this site were pooled, the average N : P ratio (21) for fresh litterfall collected in litter traps was higher than the N : P ratio (14) of canopy foliage, suggesting more P resorption relative to N. In addition, when looking at patterns among species, three of the six species resorbed significantly more P relative to N (*Symphonia globulifera*, *Brosimum utile* and *Manilkara staminodella*),

**Table 1** Resorption data from forests spanning the Sao Francisco do Para forest chronosequence in the Amazon Basin of Brazil

Forest age (yr)	N <sub>resorption</sub>	P <sub>resorption</sub>	log <sub>e</sub> (N <sub>resorption</sub> : P <sub>resorption</sub> )
6	54	65	− 0.19
20	41	53	− 0.26
40	49	59	− 0.18
200	51	73	− 0.35

With the exception of the mature forest (conservatively estimated at 200 yr old; Davidson *et al.*, 2007), all forests are secondary forests recovering after abandonment of crop fields. Data represent means of absolute N and P resorption efficiencies (%) and mean N : P resorption efficiency ratios (log<sub>e</sub> (N<sub>resorption</sub>/P<sub>resorption</sub>)) for different forest ages.



**Fig. 3** Species differences in N : P resorption efficiency ratios for six common canopy tree species at the Costa Rica site. Species represented are: *Caryocar costaricensis*; *Symphonia globulifera*; *Schizolobium parahybum*; *Brosimum utile*; *Qualea paraensis*; *Manilkara staminodella*. Different lowercase letters depict significant differences among species and white asterisks within bars denote significant differences between the absolute N and P resorption for a given species (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ). Values are means  $\pm$  1SE.

whereas no species resorbed significantly more N relative to P (Fig. 3). These results match well with other data from the site, which suggest P limitation to litter decomposition (Wieder *et al.*, 2009), soil respiration (Cleveland & Townsend, 2006) and N fixation (Reed *et al.*, 2007), as well as with the global and regional analyses described above. In addition, the data are in line with a tropical analysis of litterfall nutrient patterns from Vitousek (1984) and McGroddy *et al.* (2004).

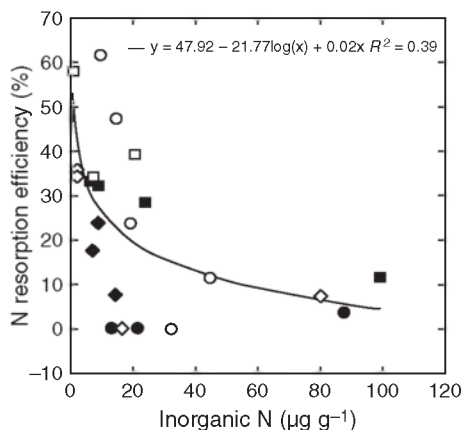
However, as with a previous analysis of foliar N : P ratios in the tropical biome (Townsend *et al.*, 2007), we observed significant species-level variation in resorption of both N and P (Fig. 3). Species variation in resorption patterns is to be expected (e.g. Killingbeck, 1984; Güsewell & Koerselman, 2003), but how do we interpret such variation within a framework of nutrient limitation? At certain sites, resorption may not lend insight into nutrient limitation: species variability could reflect variation in life history traits that have more to do with evolutionary forces and other levels of ecological organization than they do with feedbacks to nutrient status.

Alternatively, although at the individual scale nutrient resorption patterns may not predict nutrient limitation, effective integration of values across the entire community may offer more insight (as suggested for foliar N : P ratios in wetlands; Güsewell & Koerselman, 2003). For example, at the Costa Rica site, we found a great deal of variation in resorption patterns among species, but, on average, P was resorbed more strongly relative to N at the site (Fig. 3). Similar patterns emerged from the analysis of foliar N : P values by Townsend *et al.* (2007): despite enormous interspecies variation, with sufficient data, significant differences between low- and high-P fertility soils emerged. Finally, different plant species could be limited by different nutrients, even within a single site. Small-scale differences in soil nutrient availability may play important roles in regulating plant distribution and behavior (John *et al.*, 2007) – as may differences in nutrient requirements and acquisition strategies among plant species (Lambers *et al.*, 2006) – as well as temporal and spatial heterogeneity in the processes that determine nutrient gain and loss from ecosystems (e.g. Hedin *et al.*, 2009).

Finally, we found that, at the individual tree level, variations in N resorption efficiencies were negatively correlated with inorganic N concentrations of the topsoil (0–2 cm), such that lower N resorption efficiencies corresponded to higher soil inorganic N concentrations (Fig. 4), and P resorption trended towards the same pattern with soil P ( $P = 0.073$ ). This relationship could have been driven by: (1) high soil N availability leading to reduced N resorption (Stachurski & Zimka, 1975; Turner, 1977; Enoki & Kawaguchi, 1999); (2) reduced N resorption efficiencies resulting in higher quality litter (and thus faster decomposition rates; Vitousek, 1982; Wieder *et al.*, 2009) and/or larger pools of N reaching the forest floor (He *et al.*, 2011); (3) the spatial distribution of soil nutrients leading to tree species

assemblages that maintain particular nutrient resorption efficiencies (John *et al.*, 2007); or (4) any combination of these factors. With these data, we cannot discern the causes vs effects of N resorption and soil N patterns, but the relationship suggests that the coupling between N resorption and soil N status can vary not only among sites (e.g. Enoki & Kawaguchi, 1999), but also at the species and individual scale.

Overall, our analyses suggest that stoichiometric patterns of resorption may complement other plant nutrient use metrics currently employed to assess how nutrient cycling and limitation vary across a suite of environmental gradients. Considering the relative absence (and difficulty) of the direct assessment of the nature of nutrient limitation in many biomes, results obtained using a combination of indirect metrics may offer important information. The data also add to a growing body of evidence suggesting that resorption interacts strongly with other aspects of ecosystem nutrient cycling and that, even within a species, resorption can be flexible. Nevertheless, there are many questions to be answered before considering patterns in N : P resorption ratios as indicators of nutrient limitation. For example, we know that climate and stochastic environmental factors can affect resorption (Killingbeck *et al.*, 1990; Oleksyn *et al.*, 2003; Aerts *et al.*, 2007; Oyarzabal *et al.*, 2008), that resorption patterns show variable relationships with fertilization (Aerts, 1996; Vitousek, 1998) and that N and P behave very differently across gradients (Vitousek, 1982; Vitousek 1998; McGroddy *et al.*, 2004) and maintain different biochemical roles and foliar chemical forms (e.g. Ostertag, 2010). Nevertheless, nutrient resorption as a process offers a unique insight into how plants use and recycle resources, and the data presented here suggest that investigations focusing on the stoichiometry of resorption may provide a particularly exciting avenue for future research.



**Fig. 4** Relationship between topsoil inorganic N concentrations ( $\mu\text{g g}^{-1}$ ; 0–2 cm depth) and N resorption efficiencies (%) for six canopy tree species in a Costa Rican tropical rain forest ( $n = 22$ ;  $\geq 3$  per species). Regression analyses show a significant ( $P < 0.001$ ) relationship between N resorption efficiencies of individual trees and the soil inorganic N concentrations beneath their canopy. The data are best fitted with a logarithmic function. Different species are represented by different symbols: open circles, *Caryocar costaricense*; closed circles, *Symphonia globulifera*; open diamonds, *Schizolobium parahybum*; closed diamonds, *Brosimum utile*; open squares, *Qualea paraensis*; closed squares, *Manilkara staminodella*.

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